Chapter 6

Breeding For Resistance to *Phytophthora lateralis*

Authors: Richard A. Sniezko, Jay Kitzmiller, Leslie J. Elliott and James E. Hamlin June 2001

Introduction

Port-Orford-cedar lends itself exceptionally well to a program of resistance breeding. Flower production can be stimulated at an early age and establishing rooted cuttings is relatively simple, making propagation straightforward. Evaluation of some types of resistance can be done in short-term tests.

The development of populations of Port-Orford-cedar with a broad genetic base and durable resistance to *Phytophthora lateralis* is considered a key component to maintaining or restoring Port-Orford-cedar. Resistant Port-Orford-cedar is likely to be essential for the success of private owners who manage the species.

Early reports of infection of Port-Orford-cedar with *P. lateralis* indicated that all tested ornamental varieties, and some varieties of *Chamaecyparis obtusa* (Siebold and Zucc.) Siebold and Zucc. ex Endl., were susceptible while *Chamaecyparis pisifera* (Siebold and Zucc.) Endl. varieties showed resistance (Tucker and Milbrath 1942). Recent data indicate that several other species of *Chamaecyparis* are highly resistant.[10]

Initial results from resistance testing were discouraging. In early disease resistance tests that included cuttings from hundreds of trees that were phenotypically resistant in natural stands, all rooted cuttings died, indicating resistance was very low or that the inoculation level was too high, or both, to allow expression of resistance among the clones (Roth et al. 1972, Roth 1985, Zobel et al. 1985).

Up to the mid-1980s, occasional Port-Orford-cedar trees were found that survived infection or showed delayed death, but no attempts to breed for resistance or hybridize with resistant yellow cedar (*Chamaecyparis nootkatensis*) or Asiatic *Chamaecyparis* species had been attempted (Roth et al. 1987). A few survivors that have lived for an extended period of time in the presence of *P. lateralis* were noted in the cold frames near the Oregon State University (OSU) greenhouses and at the OSU Botany Farm, and were thought to represent some type of “slow dying” resistance (Roth 1985).

Work began in the early 1980s to refine an inoculation system to allow susceptible and relatively tolerant individuals to be distinguished (Hansen and Hamm 1983, Hansen and Hamm 1986). In small-scale tests using 10 individuals (four that had survived previous testing with *P. lateralis* and six new ones), resistant individuals were distinguished from susceptible individuals by a slowing of the rate of advance of the disease (Hansen et al. 1989). This was a key study in confirming resistance and leading to the initiation of further investigations and the operational breeding program for resistance by the U.S. Department of Agriculture Forest Service and the U.S. Department of the Interior Bureau of Land Management (BLM). Dr. Everett Hansen at OSU has worked with the Forest Service and the BLM since the 1980s to refine techniques to be used in operational screening efforts.

The Resistance Screening Process

Starting in 1989, the Forest Service began selecting candidate Port-Orford-cedar trees in natural stands to evaluate resistance to *P. lateralis* (fig. 6.1). The BLM began making selections in 1994 (fig. 6.2). A small number of trees in natural stands were initially selected from throughout much of the species’ range. In 1997, the program greatly expanded, and since that time more than 9,000 candidate trees, from both healthy and

[10] Sniezko, R.A. 2001. Unpublished data. On file with: U.S. Department of Agriculture, Forest Service, Dorena Tree Improvement Center, 34963 Shoreview Road, Cottage Grove, OR 97424.

diseased locales, have been selected and screened for disease resistance at Oregon State University (Bower et al. 2000). These selections have not only been from federal lands, but also from county and private lands throughout the range of Port-Orford-cedar.

Figure 6.1—Resistant Port-Orford-cedar trees growing with infected Port-Orford-cedars, growing in a natural stand

Figure 6.2—Field selection and mapping of a Port-Orford-cedar candidate tree

In the first cycle of selection (wild selections) a candidate parent tree (or clone) is selected and branches from the tree, or seedlings from seed collected from the candidate trees (1996 only) are sent to OSU for screening in a greenhouse (fig. 6.3). The samples are inoculated with *P. lateralis*. In general, two to three isolates of *P. lateralis* have been used.

In 1989 and 1990, large branches were collected and an incision was made in the branch that was then inoculated with *P. lateralis* (wound inoculation technique). Although *P. lateralis* is a root pathogen, the branch test technique was chosen for initial work (over the root methods) because many samples could rapidly be assessed and there was at least a low positive correlation with other techniques. The top resistant parents had initially been evaluated with this technique. Since 1994, however, the procedure has been to send six to 10 small branch tips to OSU, where the cut end of the branch tips are dipped in a zoospore suspension of *P. lateralis*.

When seedlings were used for testing, notably in 1996, either the stem dip technique (immersing the bottom two centimeters of a cut portion of the seedling in a zoospore suspension) (fig. 6.4) or a root dip technique (immersing the bottom two centimeters of the container containing the seedling roots in a zoospore suspension) was used. In the stem dip technique, the length of the lesion growth on the sample stem is measured several weeks after inoculation, with lesion length representing a possible measure of resistance. For the root dip technique, time until mortality is recorded (fig. 6.5).

Figure 6.3—Collecting branches for resistance screening

Figure 6.4—Stem dip technique for inoculating samples for testing resistance to *Phytophthora lateralis*

Figure 6.5—Seedlings being monitored for survival after inoculation with the root dip technique

In general, a high resistance checklot (PO-OSU-CF1) has been included in the testing since 1993 and a low resistance checklot (PO-OSU-CON1) since 1997 to provide a basis of comparison. These checklots are used to help determine which parent trees are initially selected for the breeding program and for further testing. Due to the large number of selected trees screened since 1997, the screening has been done in many groups or "runs" spread throughout the year. The stem dip technique was chosen for the initial phase of operational screening because it allows for a rapid assessment of differences among parent trees for at least one type of resistance potential.

Resistance Screening Results

Through the year 2000, researchers have identified 1,179 potentially disease resistant trees based upon the initial phase of screening using a branch lesion test (table 6.1). For detail on screening methods used see Appendix E. The resistance identified to date in the branch lesion test is not expressed as immunity, but as reduced growth rate of the fungus in infected trees.

In screenings with different methods over the years, several clones (notably PO-OSU-CF1) from Coos County in Oregon, and clone 510015 from the Gasquet Ranger District, Six Rivers National Forest in California have consistently been rated best or near the top for small lesion scores (Sniezko and Hansen 2000; Sniezko et.al. 2000). Recent seedling trials indicate that Parent 117490, from the Gold Beach Ranger District in Oregon, shows much higher resistance (percent survival) than any selection to date (table 6.2).

Based on selections prior to 1997, it appears that there are relatively few clones (perhaps 1 to 2 percent) that repeatedly stand out in all screening tests. The remainder of the clones may have resistance, but it may be more subtle and not apparent under heavy inoculum loads or without a more sensitive test. A study to examine the possible mechanisms of resistance has been initiated and may provide insight to a more definitive evaluation of resistance.

Table 6.1—Number of Port-Orford-cedar selections for breeding from initial resistance screening

	Number of Selections Tested									
	1989	**1990**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**Total**
Medford BLM			20	30	99	4	19		6	**178**
Roseburg BLM					30	13	2		5	**50**
Coos Bay BLM				10	39	112	20		1	**182**
Salem BLM									1	**1**
FS Siskiyou NF	10	40		28	203	121	21			**423**
FS Siuslaw NF							5			**5**
FS California									6*	**6**
FS Klamath NF					3	10	3			**16**
FS Six Rivers NF	3	10		34	3	3	1	2		**56**
FS Shasta-Trinity NF				27			1			**28**
Non-federal Lands				19	6		152	8	49	**234**
Total	**13**	**50**	**20**	**148**	**383**	**263**	**224**	**10**	**68**	**1179**

*Specific National Forest (NF) information not available in database as of 3/17/03

Table 6.2—Percent mortality after one year for three test methods for six of 44 open-pollinated seedling families tested in 2000

Parent	Greenhouse Root Dip (OSU)	Test Location Raised Bed (OSU)	Camas Valley (BLM Field Site)
117490	0	38.9	8.3
510005	25.0	33.3	0
CF1	50.0	50.0	25.0
117499	83.3	66.7	50.0
510044	66.7	75.0	75.0
70102	100	91.7	100

Validation of the Screening Process

Greenhouse screening techniques developed at OSU, such as the stem and root dip techniques, are methods to survey many candidate trees quickly for an indication of relative resistance. Artificial inoculation and subsequent assessment is quicker, less expensive, and more controllable than field plantings. Little is known, however, about how these measures relate to resistance in the field and how much longer the more resistant seedlings may survive under field conditions. OSU established a small field planting in 1989, while plantings have been established by the Forest Service and BLM since 1993 to validate screening methods and examine the durability and types of resistance (Sniezko and Hansen 2000). Although current evidence indicates that there is little genetic variation in *P. lateralis* (see Chapter 3), these plantings will allow tested material to be evaluated and compared under a range of conditions. Using this information, a more comprehensive comparison between field and greenhouse results can then be made.

In 1999, the process of re-testing the initial stem dip selections using the root dip technique began. Results from the first parents tested using rooted cuttings showed that a subset appears to have resistance comparable to the high resistance control (CF1). Preliminary testing in 1996 showed only a low positive correlation between the stem and root dip methods (Appendix E). This second phase of testing will either: (a) establish a sufficient correlation between the stem and root dip techniques to validate the initial screening results, or (b) provide a further screening of the initial selections.

Field plantings have demonstrated that rooted cuttings or open-pollinated seedlings from some of the parents showing high resistance to *P. lateralis* (in the initial branch and stem dip testing process) have much higher survival than those of the parents rated low for resistance (fig. 6.6). Most of the mortality in the field tests appears to occur in the first two years. Microsite variation can be substantial and may contribute to early mortality. Eleven years after planting, rooted cuttings from the most resistant parents have shown 50 to 80 percent survival in the field (Sniezko and Hansen 2000, Sniezko et al., n.d.), while cuttings from nonresistant parents have generally shown 0 to 5 percent survival; in the earliest tests open-pollinated seedlings from the most resistant parents have shown 25 to 50 percent survival versus 0 to 35 percent for other parents. Detail on validation plantings is presented in Appendix F.

Figure 6.6 – Field plantings of high resistance genotypes

Common Garden Study

Common garden studies are sites where the same genetic stock is planted across a range of different sites that vary in elevation and latitude and longitude. As stated in Chapter 5, a common garden study using range-wide material was established in 1996 to evaluate the genetic variability of Port-Orford-cedar (Kitzmiller and Sniezko 2000). This study examined both height growth and disease resistance traits. Disease resistance was evaluated using two methods: (1) a stem dip test where branch tips from a selected tree were dipped in a zoospore suspension of *P. lateralis* and (2) a root dip test where a seedling's roots were immersed in a zoospore suspension. Details on study design are presented in Chapter 5.

Geographic Variation in Resistance Traits

Compared to height growth, disease resistance traits (based upon stem and root dip tests) showed much weaker, though significant, geographic patterns of variation. This is not surprising because the disease has apparently spread only recently into the native range of Port-Orford-cedar. There has not been sufficient time of coexistence of host and pathogen to co-evolve a strong geographic pattern across the range of habitats. To assess the overall geographic pattern, height growth plus disease resistance variables were combined in a canonical correlation analysis with three geographic origin variables (latitude, longitude, and elevation) expressed in a full quadratic model. Comparing the amount of variation explained by geographic factors for allozyme diversity and the amount of variation explained for common garden height growth, (Millar et al. 1992, unpublished range-wide study), R2 = 13.5 percent for the former and R2 = 75 percent for the latter. Clearly the geographic variation pattern is far greater for height than for allozymes.

In a 1996 test of random parents (not selected for field test resistance) from much of the range of Port-Orford-cedar, patterns of variability differed both at the stand and watershed level.

Root test resistance showed greater geographic variation than stem test resistance, and was almost opposite for geographic pattern. Root test resistance decreased from the coast to inland sites, and to a lesser degree, from north to south. Root test resistance was higher for the moist northern and coastal sources and was lower for the drier southern and inland sources. Stem test resistance increased from north to south. Southern latitude sources had smaller stem lesions than northern latitude sources. Stem test resistance increased with increasing elevation of a source and with distance from the coast. Further investigation is needed, but these trends may indicate that some parts of the range of Port-Orford-cedar may have a higher frequency of resistance and/or that different resistance mechanisms may be in higher frequency in parts of the species range.

Phenotypic Correlations Among Traits

For root test resistance, on a stand mean basis, 10 percent of the variation was positively associated with early height growth. For stem test resistance, on a stand mean basis, eight percent of the variation was negatively associated with early height growth (two percent on family mean basis). Thus, to a small but significant extent, stands and trees that grow fast tend to possess higher root test resistance. To a lesser extent, stands and trees that grow slow tend to possess higher stem test resistance.

For stand means the correlation between root test resistance and stem test resistance was non-significant. Thus, stands cannot generally be found to have both types of resistance. However, a small but significant portion of families may have both types of resistance.

Variation in Disease Resistance at the Watershed Level

The genetic component for root test resistance accounted for 58.6 percent of the total variability: watersheds 14.1 percent, stands within watershed 7.5 percent, and families within stand within watershed accounted for 37 percent. All three were highly significant. Blocks and random plot error made up the remaining variability.

For stem test resistance, the genetic component was small (14.3 percent of the total). Like root test resistance, the families within stand within watershed component (9.7 percent) for stem test resistance was much greater than the watershed (2.5 percent) and stand (2.1 percent, non-significant) components. Blocks and plot error made up the majority (85.7 percent) of the total variability for stem-test resistance.

Therefore, the genetic basis for root test resistance is far greater than it is for stem test resistance, and resistance varies mostly from family to family within a watershed. By contrast, for height growth the watershed component was several times greater than the families within stand within a watershed.

Variation in Disease Resistance at the Breeding Zone Level

A slightly larger portion of the total variability (61 percent) is attributed to breeding zones (see Chapter 5 for a discussion of breeding zones) than to watersheds. Breeding zones accounted for 18.1 percent and seed zones within breeding zones were non-significant at 2.4 percent. Families within seed zones within breeding zones were by far the most variable at 40.3 percent of the total. For stem test resistance, neither breeding zones nor seed zones were significant. Families within zones accounted for 11.9 percent of the total variability, and blocks plus plot error contributed the majority (85.5 percent).

Breeding Program

In the early 1990s, the Forest Service and BLM began a breeding program with Port-Orford-cedar to attempt to increase resistance to *P. lateralis*. This species lends itself exceptionally well to a program of resistance breeding (Elliott and Sniezko 2000) because it is easily propagated. Propagation techniques used at Dorena Tree Improvement Center, Cottage Grove, Oregon, are described below.

Controlled Pollination

Port-Orford-cedar can be induced to flower at most times of the year as long as they are not dormant. Growth hormones, such as gibberellins, can be used to induce flowering, and in combination with photoperiod at the timing of treatment(s), can be used to effectively influence the relative amounts of male and female flowering (Zobel et al. 1985). Flowering in Port-Orford-cedar can be induced in trees less than one year old.

Controlled pollination is an essential part of the breeding and resistance-screening program at Dorena Tree Improvement Center (DTIC). The process is summarized below.

To stimulate cone production in young material, a foliar spray application of gibberellic acid (GA3) is applied in June. The treatment is applied weekly, over a five-week period, at a rate of 100 mg of GA3 per liter of water. Large increases in strobili are generally evident the year following treatment. Large clonal differences exist in the amount of strobili produced (Elliott and Sniezko 2000).

Pollen is shed (at Dorena) from late February through mid-April (fig. 6.7). Pollen is collected and dried for 24 to 48 hours at 15 to 20 C and 20 to 40 percent relative humidity. For short-term storage, pollen is refrigerated with a desiccant. For long-term storage, pollen is stored in a freezer at -14 C. The average viability of pollen collected in 1997 and 1998 was 51 and 72 percent, respectively. There was a large clonal variation in viability, with a range from zero to 93 percent. Storage up to two years does not appear to significantly reduce viability.

Figure 6.7—Pollen shed by Port-Orford-cedar growing at Dorena Tree Improvement Center, Cottage Grove, Oregon

Controlled pollination is initiated at the first sign of receptivity by the female strobili (pollen drop). Because of the variability in timing of receptivity, two pollinations are usually attempted for each cross within a four to seven day period. Although there is clonal variability, observation shows the majority of pollen shedding occurs a week ahead of the time when most female strobili become receptive on the same tree (which would minimize natural self-pollination).

Conelet abortion may be substantial during the development period (March through September). For example, in 1997, there was a 30 percent conelet abortion rate at DTIC. In 1997 through 1999 the overall average percent filled seed from control crossings ranged from 40 to 50 percent and the average filled seed per cone ranged from 5.0 to 6.2.

Selfing (breeding an individual with itself) does produce viable seed. However, at DTIC, a reduction in percent filled seed and number of seeds per cone has been evident. For example, in 1997, selfing produced an average of 22 percent (range, 0 to 76 percent) filled seed, while outcrosses produced an average of 51 percent (range, 0 to 94 percent). Selfing averaged 2.8 filled seeds per cone (range, 0 to 11.7) and outcrosses, 6.7 filled seeds per cone (range 0 to 11.2).

Vegetative Reproduction

Cuttings from Port-Orford-cedar are easily rooted. For example, at DTIC, in 1998, 96 percent of the 330 clones where rooting was attempted were successfully rooted. Rooting time varied for seedlings, and ranged from 3 to 12 months. Rooting success and times vary with age; younger material roots more readily. Rooting success is improved if material is collected when it is dormant or has slowed growth (November through February). Cuttings from major branches in the lower portion of the crown are preferred (Zobel 1990a).

Summary

Port-Orford-cedar is the species most adversely affected by *P. lateralis*. While preliminary results from the breeding and testing efforts indicate there may be sufficient levels of resistance within Port-Orford-cedar to begin a breeding program, other avenues are also being examined. A preliminary screening of several other species and hybrids has begun to evaluate their resistance and learn more about resistance mechanisms and their inheritance.

A containerized seed orchard was established at the Dorena Tree Improvement Center, with material from the more resistant selections from the screening process (fig. 6.8). The goal of the breeding program includes developing durable resistance as well as keeping diverse genetic populations available to ensure general adaptation throughout the native range of Port-Orford-cedar. A preservation orchard was established in 1998 at the BLM Tyrrell Seed Orchard in Lorane, Oregon to also help maintain diverse genotypes. Excellent inter-regional and interagency cooperation as well as input from other groups, coupled with current knowledge of the biology of Port-Orford-cedar and resistance to the exotic pathogen, *P. lateralis*, should allow for rapid progress in evaluating and potentially developing resistant populations. Flower production can be stimulated at an early age and establishing rooted cuttings is relatively simple. Control pollinations on earlier selections began in 1996 and the full-sibling progenies are now undergoing resistance testing.

Figure 6.8—Containerized seed orchard at the Dorena Tree Improvement Center, Cottage Grove, Oregon

The operational breeding program for *P. lateralis* resistance is still young; however, results from recent testing and the biology of Port-Orford-cedar lead one to be cautiously optimistic of the potential for developing durable resistance. Only a few parents from the initial stem dip screening process have been identified with resistance sufficient to consider for immediate regeneration and restoration plantings; however, since 2000 the number of parents has been increasing dramatically as results from root dip testing and field validations are finalized. Additional resistant parents are likely to be identified based on results from current trials and additional information on the mechanisms of resistance. The use of containerized orchards allows easy upgrading of the orchards for genetic diversity and resistance as more testing is completed. Orchards can be established by breeding zones to help ensure localized adaptability. Some resistance mechanisms may not be 'strong' enough to be durable in the field without further breeding. Breeding can increase the overall resistance and incorporate any appropriate resistance mechanisms.

New data are being generated rapidly from the resistance-breeding program. Updates are presented at scientific meetings and overviews posted on the Dorena website: www.fs.fed.us/r6/dorena. A breeding program can provide sufficient quantities of seed to meet the demand of public and private organizations for highly resistant seedlings. Subsequent efforts could concentrate on making resistant seed available for additional breeding zones, increasing both the genetic diversity of the orchards and level of resistance. An additional benefit of the program could be to make resistant material available to the horticulture industry where Port-Orford-cedar was once a significant contributor in the Pacific Northwest.

Genetic resistance is one tool in the overall management strategy for Port-Orford-cedar and is best used in conjunction with other management tools mentioned elsewhere in this document.

Literature Cited

Bower, A.D.; Casavan, K; Frank, C.; [et al]. 2000. Screening Port-Orford-cedar for resistance to *Phytophthora lateralis*: results from 7000+ trees using a branch lesion test. In: Hansen and Sutton, eds. Proceedings of the first international meeting on *Phytophthoras* in forest and wildland ecosystems, IUFRO Working Party 7.02.09. Corvallis, OR: Oregon State University, Forest Research Laboratory: 99-100

Elliott, L.; Sniezko, R.A. 2000. Cone and seed production in Port-Orford-cedar container orchard. In: Hansen and Sutton, eds. Proceedings of the first international meeting on *Phytophthoras* in forest and wildland ecosystems, IUFRO Working Party 7.02.09. Corvallis, OR: Oregon State University, Forest Research Laboratory: 105-106.

Hansen, E.M.; Hamm, P.B. 1983. Resistance screening of Port-Orford-cedar to *Phytophthora lateralis* root rot. Corvallis, OR: Oregon State University. Unpublished report. 17 p. On file with: Southwest Oregon Forest Insect and Disease Service Center, J. Herbert Stone Nursery, 2606, Old Stage Road, Central Point, OR 97502.

Hansen, E.M.; Hamm, P.B. 1986. Screening Port-Orford-cedar for resistance to *Phytophthora lateralis*. Corvallis, OR: Oregon State University. Unpublished report. 26 p. On file with: Southwest Oregon Forest Insect and Disease Service Center, J. Herbert Stone Nursery, 2606, Old Stage Road, Central Point, OR 97502.

Hansen, E.M.; Hamm, P.B.; Roth, L.F. 1989. Testing Port-Orford-cedar for resistance to *Phytophthora*. Plant Disease 73(10):791-794.

Kitzmiller, J.H.; Sniezko, R.A. 2000. Range-wide genetic variation in Port-Orford-cedar (*Chamaecyparis lawsoniana* [A. Murr.] Parl.). I. Early height growth at coastal and inland nurseries. Frontiers of Forest Biology: Proceedings of the 1998 joint meeting of the North American Forest Biology Workshop and the Western Forest Genetics Association. Journal of Sustainable Forestry. 10:57-67.

Millar, C.I.; Delany, D.L.; Westfall, R.D. 1992. Genetic diversity in Port-Orford-cedar: range-wide allozyme study. Administrative report. 4 p. On file with: Southwest Oregon Forest Insect and Disease Service Center, J. Herbert Stone Nursery, 2606, Old Stage Road, Central Point, OR 97502.

Roth, L.E. 1985. Inoculation methods for quantitatively evaluating the response of Port-Orford-cedar trees to *Phytophthora lateralis*. Corvallis, OR: Oregon State University. Unpublished report. 26 p. On file with: Southwest Oregon Forest Insect and Disease Service Center, J. Herbert Stone Nursery, 2606, Old Stage Road, Central Point, OR 97502.

Roth, L.F.; Bynum, H.H.; Nelson, E.E. 1972. *Phytophthora* root rot of Port-Orford-cedar. Forest Pest Leaflet 131. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 7 p.

Roth, L.E.; Harvey, R.D. Jr.; Kliejunas, J.T. 1987. Port-Orford-cedar root disease. Forest Pest Management Report No. R6 FPM-PR-294-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Region 6. 11 p.

Sniezko, R.A.; Hansen, E.M. 2000. Screening and breeding program for genetic resistance to *Phytophthora lateralis* in Port-Orford-cedar (*Chamaecyparis lawsoniana*): early results. In: Hansen and Sutton, eds. Proceedings of the first international meeting on *Phytophthoras* in forest and wildland ecosystems, IUFRO Working Party 7.02.09. Corvallis, OR: Oregon State University, Forest Research Laboratory: 91-94.

Sniezko, R.A.; Hansen, E.M.; Kitzmiller J.H.; and Hamlin J. [N.d.]. Range-wide genetic variation in *Phytophthora lateralis* resistance in *Chamaecyparis lawsoniana*. Manuscript in preparation. Dorena, OR: U.S. Department of Agriculture, Forest Service, Dorena Genetic Resource Center. On file with: Southwest Oregon Forest Insect and Disease Service Center, J. Herbert Stone Nursery, 2606, Old Stage Road, Central Point, OR 97502.

Tucker, C.M.; Milbrath, J.A. 1942. Root rot of *Chamaecyparis* caused by a species of *Phytophthora*. Mycologia. 34:94-103.

Zobel, D.B. 1990. *Chamaecyparis lawsoniana* (A. Murr.) Parl., Port-Orford-cedar. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America: conifers. Agricultural handbook 654. Washington, DC: U.S. Department of Agriculture Forest Service. Vol. 1: 88-96.

Zobel, D.B.; Roth, L.F.; Hawk, G.M. 1985. Ecology, pathology, and management of Port-Orford-cedar (*Chamaecyparis lawsoniana*). General Technical Report PNW-184. Portland, OR: U.S. Department of Agriculture, Forest Service Pacific Northwest Forest and Range Experiment Station. 161 p.